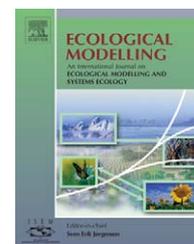


available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)

# Lion, wildebeest and zebra: A predator–prey model

Temple H. Fay, Johanna C. Greeff\*

Department of Mathematical Technology, Tshwane University of Technology, P/Bag X680, Pretoria 0001, South Africa

## ARTICLE INFO

### Article history:

Received 13 November 2004  
 Received in revised form 29  
 November 2005  
 Accepted 1 February 2006  
 Published on line 5 April 2006

### Keywords:

Mutualism  
 Functional response  
 Cropping

## ABSTRACT

In this paper, we describe our attempts to fit historical data from the Kruger National Park with a plausible one predator and two mutualistic prey model. Explicit examples of how a model is being developed, improved and tested are rare in literature. This is probably because of the many uncertainties, shortcomings in data, assumptions, speculations and intuitive decisions that form part of the process, which provokes a deep and well-founded fear of the resulting model being criticized. We investigate the effects of including or excluding various phenomena present in population interactions in order to mimic a real world situation. This allows for gaining insight into the behaviour of the system and possible projections of future trends that can be expected. We hope to set a simple yet practical example that may be useful to young researchers and in the educational situation, where computer models are progressively becoming an integral part.

© 2006 Elsevier B.V. All rights reserved.

## 1. Introduction

In the Kruger National Park, South Africa, the central grasslands have supported huge herds of zebra and wildebeest for many years; the lion was and continues to be their principal predator. During the dry period 1969–1972, these grazer species had to be cropped because of over-utilization of vegetation. Zebra were cropped more severely and for a longer period. When cropping was ceased in 1972 after a season of heavy rains, the zebra population declined for a period as expected, and then recovered steadily, while the wildebeest population kept on declining in spite of plentiful graze (Starfield et al., 1976). In this article, we assess what has occurred in the central region of this park after the cropping of wildebeest and zebra was interrupted. Note that no data on the age structure of the species under discussion is available, and the fecundity rates for each age group cannot be deduced from the data. The more widely used discrete approach to modelling population interaction, using difference equations and Leslie matrices, is therefore not suitable in this case. Hence, in our quest to gain insight into what we observe, we use continuous

models consisting of differential equations, since population sizes are large enough (generally taken as larger than 1000) to justify a continuous approach.

Predator–prey models (continuous and discrete) have been widely studied in the literature, some of which discuss the effect of mutualism, competition, harvesting and predation in a multi-species system. Recently, for example, Costa et al. (2000) carry out an analysis of both one prey one predator Lotka–Volterra and Leslie–Gower with a weighted escape-harvesting property. A computable general equilibrium approach is developed and applied to model multiple prey and predators in Tschirhart (2004). Features in this model include predators and prey maximizing net energy intake by responding to energy expenditures for capturing prey and no functional response assumptions are made. Gui and Ge (2005) discuss a two species predator–prey model with two life stages, immature and mature, with harvesting of the mature populations. A simulation technique employing statistics and a matrix perturbation analysis called the life-stage simulation analysis is developed in Wisdom et al. (2000) to measure possible effects of uncertainty and variation in rates of population

\* Corresponding author. Tel.: +27 12 3186326; fax: +27 12 3186114.

E-mail addresses: [thfay@hotmail.com](mailto:thfay@hotmail.com) (T.H. Fay), [greeffjc@tut.ac.za](mailto:greeffjc@tut.ac.za) (J.C. Greeff).  
 0304-3800/\$ – see front matter © 2006 Elsevier B.V. All rights reserved.  
 doi:10.1016/j.ecolmodel.2006.02.026

growths specifically for purposes of conservation and planning. Other recent literature references include Azar et al. (1995), Dai and Tang (1998), Křivan (1998), Song and Chen (2002), and texts by Jørgenson (1988) and Murray (1993), just to name a few. However, the literature detailing the process of model construction from first assumptions to a final complex model is difficult to find. This paper gives a step-by-step description of the developmental phases for a specific case, which may prove useful to students and others interested in ecological modelling. The interested reader can find a wealth of information by going to the Ecological Modelling web page or using the search engine Science Direct.

To our knowledge there is no recognized three species model that specifically describes interaction between one predator and two mutualistic prey, to which the results of our model could be compared. The challenge therefore is to adapt general theoretical models for multiple species in order to postulate and investigate mathematically the effect of introducing terms that represent various phenomena, such as mutualism, seasonal calving and functional response. We find a reasonable fit to the available data over the period 1972–1987, and apply our newly obtained knowledge to anticipate possible future trends. The models used to describe the population dynamics in this study are extremely simple and conservative, considering all the variables that can have an effect on the dynamics of populations. Nevertheless, they suggest directives for action.

## 2. Biological background

The Kruger National Park is situated at the southern end of Africa, on the international border between South Africa and Mozambique. According to Starfield et al. (1976) the central part of the reserve is well suited for various species of grazers and capable of sustaining approximately 12,000 zebra (*Equus burchelli*) and 12,000 wildebeest (*Connochaetes taurinus*). There are various predator species present in Kruger Park, but lion (*Panthera leo*) has the greater impact on the wildebeest and zebra population numbers (Bothma-Du Preez, 1996). In Table 1, population census numbers of wildebeest and zebra are given for the period 1972–1994, while the lion population has been more or less sustained at approximately 300–500 by migrating nomads (Smuts, 1982). The steep decline in wildebeest numbers after cropping was terminated in 1972, and very slow recovery even after 10 years were apparent reasons for concern.

In 1975, a harvesting programme on the lion population was implemented in an effort to allow the wildebeest population to recover. This was discontinued in 1982 after it was realized that nomad lions immigrate to the central parts of the park to replenish the population as soon as zebra and wildebeest numbers picked up (Smuts, 1982).

Two species models describing predator–prey, mutualism or competition situations are well known and are discussed in many texts. For a good mathematical analysis of the continuous approach using systems of differential equations, the reader is referred to Boyce and Diprima (1992) and Murray (1993). Specific deterministic models describing multiple species interaction are not as widely discussed in literature

**Table 1 – Wildebeest, zebra and lion population densities since 1972**

Year	Wildebeest	Zebra
1968	14000	14000
1970	11800	12400
1972	10600	10500
1974	7931	7523
1975	6745 <sup>a</sup>	7850
1976	5783	7616
1977	5066	7649
1978	5141	8316
1979	5502	8511
1980	5816	8877
1981	6512	10834
1982	8127	11603
1983	7584	9807 <sup>a</sup>
1984	8062	12830
1985	8634	11822
1986	9406	12520
1987	9915	13097
1988	9650	12431
1989	9547	13008
1990	9807	12176
1991	9788	13240
1992	10574	12060
1993	10658	13577
1994	11243	13004

<sup>a</sup> Possible undercounts because of high grass during good seasons.

as their stochastic counterparts, although the theory on finding qualitative solutions to two or three species models allows for fruitful investigations in terms of stability. The well-known Lotka–Volterra equations generically expressed by

$$\frac{dX_i}{dt} = X_i \left( b_i + \sum a_{ij} X_j \right), \quad i, j = 1, 2, \dots, n$$

lend themselves to be adapted to describe the dynamics of  $n$  interacting species in a community. Rates of change in the population size of each of the  $n$  species are represented by the equations where  $b_i$  describe the intrinsic population growth (in which case the sign of  $b_i$  would be positive) or decline (sign of  $b_i$  negative) in the absence of the other species, while the signs of  $a_{ij}$  would reflect whether species interact in terms of predation, competition or mutualism.

Consider an example where species  $X_2$  predaes on species  $X_1$  and  $X_3$ , while species  $X_1$  and  $X_3$  are in a mutualistic relationship. A general but very simplistic model for these three species is

$$\begin{aligned} \frac{dX_1}{dt} &= X_1(b_1 - a_{12}X_2 + a_{13}X_3), & \frac{dX_2}{dt} &= X_2(-b_2 + a_{21}X_1 + a_{23}X_3), \\ \frac{dX_3}{dt} &= X_3(b_3 - a_{32}X_2 + a_{33}X_3) \end{aligned}$$

where the constants  $a_{ij}$  and  $b_i$  are positive. Modifications may be introduced to this general model in order to describe specific dynamics present in a multi-species community more accurately, for example:

- On first impression it seems that  $a_{ij}$  and  $b_i$  are all constants, but these parameters could be functions of one or more of the  $X_i$ 's (Pimm, 1991).

- Should species  $X_i$  experience an over-crowding problem, members of the same species compete for food and logistic growth patterns become applicable. This intra-species competition can be indicated with introducing carrying capacity constraints, or by a term  $-c_i X_i^2$  added to the equation reflecting the behaviour of species  $X_i$ .
- The system above suggests a linear functional response, that is, predators will consume prey at a rate proportional to the number of prey available. This is of course not true. A more realistic assumption is that predators will eventually only kill the number of prey they can consume according to their own numbers. This is referred to as a Type II functional response, as discussed by [Arditi and Ginzburg \(1986\)](#), and [Holling \(1965\)](#).

### 3. Developing a model for lion, wildebeest and zebra

We have used constant values for the parameters of the model in this exercise. We know that some of these constants are nothing more than reasonable guesses, so we are wary of trusting what the computer model reproduces. They are treated qualitatively, as a vehicle for the logic to postulate a qualitative argument, which may prove to be robust if different values are used. This is discussed in a follow-up article by the same authors. We have initially constructed two predator–prey models and two logistic growth models, and tested their accuracy against available field data, obtaining good fits. The method followed to determine estimates of the parameters in these models are based on census numbers, multiple regression analysis and information and suggestions offered by field specialists, as discussed in depth by [Fay and Greeff \(1999a\)](#). The interested reader may also consult [Hilborn and Mangel \(1997\)](#) on an alternative approach to estimating parameter values and assessing the accuracy thereof.

Let  $\frac{dx}{dt}$  describe the rate of change in the wildebeest population,  $\frac{dy}{dt}$  the rate of change in the lion population, and  $\frac{dz}{dt}$  is the zebra population changes over time. The predator–prey models for lion–wildebeest and lion–zebra are respectively

$$\begin{aligned} \frac{dx}{dt} &= 0.405x - 0.81xy, & \frac{dy}{dt} &= -1.5y + 0.125yz, \\ \frac{dy}{dt} &= -1.5y + 0.125xy, & \text{and} & \frac{dz}{dt} = 0.35z - 0.75yz \end{aligned}$$

while logistic growth equations for wildebeest and zebra in the absence of a predator are

$$\frac{dx}{dt} = 0.405x \left(1 - \frac{x}{12}\right) \quad \text{and} \quad \frac{dz}{dt} = 0.34z \left(1 - \frac{z}{12}\right)$$

Assumptions and other factors of importance for these models are:

- For the traditional predator–prey models it is assumed that only two species are present in the interaction situation and that food is plentiful for the prey species.
- All exterior factors that may affect the dynamics of these species, such as droughts, fires and epidemics, are assumed

to be stable for the period under discussion, or at least have a similar effect on the interacting species.

- We prefer to use continuous models since the populations are large enough, no distinction is made between age groups of a species, and continuous models in this case are much more accurate in describing the population variations over time than their discrete counterparts.
- Throughout the exercise, all results indicate population sizes measured in thousands. The population densities are indicated on the vertical-axis, and time on the horizontal-axis in all figures.
- Accurate census numbers for lion in the region over this period are not available, but officials roughly estimate that 300–700 lion, sustained by migration, were present in the area at any given time, depending on prey availability. We assume an initial population of 500 lion throughout the exercise.
- The lion–wildebeest model has a centre critical point at (12;0.5), indicating a stable population pair of 12,000 wildebeest and 500 lion, while the lion–zebra model stabilizes at the centre (12;0.425), representing 12,000 zebra and 425 lion. These correspond well to the available field data.
- The parameter 0.125 of both the predator–prey interaction terms  $xy$  and  $yz$  in the equations describing the dynamics of the lion population refers to the capability of the predator to convert food into (positive) reproduction. For more details on how this is calculated, see [Fay and Greeff \(1999a\)](#).
- Wildebeest and zebra do not compete for food; therefore in the absence of lion their population dynamics are governed by independent logistic growth equations. The changes in their population sizes depend on the intrinsic growth rates and carrying capacities for each species. The carrying capacity of the area is taken as 12,000 for both wildebeest and zebra under normal conditions ([Starfield et al., 1976](#)).

In the next section, we experiment with a three species model and explore various venues in an attempt to explain mathematically the dynamics represented by the census numbers of lion, wildebeest and zebra. These models describe the interaction between one predator and two mutualistic prey species, with initial populations 10,600, 10,500 and 500 for wildebeest, zebra and lion, respectively, as was the case at the end of 1972 when cropping of wildebeest and zebra was terminated, and cropping of lion was considered.

#### 3.1. Simplistic approach with mutualism

On first intuition, we follow the simplistic approach and combine the above systems. Since there is now a predator present that will have an effect on the wildebeest and zebra numbers, we neglect logistic growth for the moment but introduce mutualism. Mutualism between the wildebeest and zebra (described by the  $xz$ -terms in the model) can be attributed to the fact that they do not compete for food but usually graze in mixed herds, finding safety in numbers from common predator attacks. [Smuts \(1982\)](#) and [Bothma-Du Preez \(1996\)](#) report that lion consume more wildebeest (28% of its diet) than zebra (19%) since the latter carry more meat and lion are more successful in killing a wildebeest per interaction due to the size of

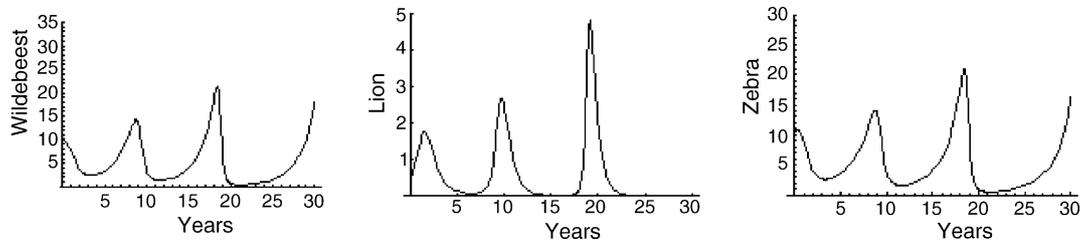


Fig. 1 – Simplistic approach with mutualism: equilibrium at (5.95,0.61,6.04) is a rejecting spiral point.

the animal compared to that of zebra. However, this “safety in numbers” is probably almost insignificant, hence the parameter values representing mutualism should be very small and are estimated at 0.015 and 0.02 for wildebeest and zebra, respectively, to obtain a reasonable fit of the model to the data. (Sensitivity, or rather insensitivity, of model behaviour to these parameter estimates is discussed in Fay and Greeff, 2006.) The resulting three species model is

$$\begin{aligned}\frac{dx}{dt} &= 0.405x - 0.81xy + 0.015xz, & \frac{dy}{dt} &= -1.5y + 0.125(xy + yz), \\ \frac{dz}{dt} &= 0.34z - 0.75yz + 0.02xz\end{aligned}$$

A mathematical analysis of the system shows that there is only one critical point situated at (5.95;0.61;6.04) in the population quadrant, referring to a population pair of 5950 wildebeest, 610 lion and 6040 zebra. These population sizes do not correspond favourably to the field data of say after 15 years. Furthermore, when inspecting the eigenvalues of the linearized system at this critical point, we find it to be an unstable repelling spiral point. The population-time graphs in Fig. 1 confirm this, showing ever-increasing fluctuations, with almost-extinction followed by extreme (but unrealistic) growth of all three populations over a time.

This is a classical example of the aggregation problem that arises when one attempts to model the total function of a group of diverse species in the behavioural form of a single species. Overton (1984, p. 51–68) warns that one should not attempt to model the behaviour and function of the assemblage as a combination of individual parts. He states that this is rarely successful, as the resolution usually causes changing levels of interaction. Since specific models for similar situations are not readily available in literature, we need to speculate and experiment with our model and introduce interaction terms that could represent interaction under these circumstances.

### 3.2. Modify equation for lion dynamics

The existing model lends itself to modification, if the changes can be properly justified. Our next attempt is to modify the equation describing the dynamics of the lion population by introducing the factors 0.81 and 0.75 to the  $xy$  and  $xz$  terms, respectively. This is justified by reasoning that the capability of the predator to convert food successfully will be subjected to per ratio interaction with the two respective prey populations.

The model is

$$\begin{aligned}\frac{dx}{dt} &= 0.405x - 0.81xy + 0.015xz, \\ \frac{dy}{dt} &= -1.5y + 0.125(0.81xy + 0.75yz), \\ \frac{dz}{dt} &= 0.34z - 0.75yz + 0.02xz\end{aligned}$$

This does not solve the problem. Eigenvalue analysis confirms that we still have only one critical point in the population quadrant, with slightly increased values, and again this is a rejecting spiral predicting extinction of all three species.

### 3.3. Logistic approach (with mutualism)

We now consider re-introducing logistic growth to the wildebeest and zebra equations, assuming that intra-species competition in nature cannot be ignored as over-population of a prey species is still possible, even in the presence of predators. The model with inclusion of logistic growth now is

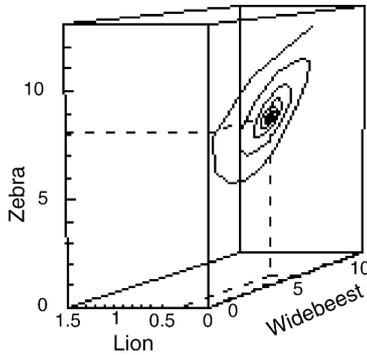
$$\begin{aligned}\frac{dx}{dt} &= 0.405x \left(1 - \frac{x}{12}\right) - 0.81xy + 0.015xz, \\ \frac{dy}{dt} &= -1.5y + 0.125(xy + yz), \\ \frac{dz}{dt} &= 0.34z \left(1 - \frac{z}{12}\right) - 0.75yz + 0.02xz\end{aligned}$$

The introduction of these logistic terms changes the nature of the critical point in the population quadrant radically. We now have a stable critical value at (7.336;0.343;8.076) indicating 7336 wildebeest, 343 lion and 8076 zebra. Confirming the existence of an attracting spiral point, the solution trajectory shown in Fig. 2 slowly spirals in to this stable point.

Unfortunately, it takes approximately 80 years for the populations to stabilize—much too long to be accurate even when all exterior factors are assumed to be stable. Also note that the wildebeest and zebra populations settle way below the carrying capacity, which does not correspond to the field data. The lion population experiences wild fluctuations in this model, also not seen in the data.

### 3.4. Type II functional response (with mutualism and logistic approach)

In an attempt to address these imperfections of the model, we import a limiting factor in the form of functional response



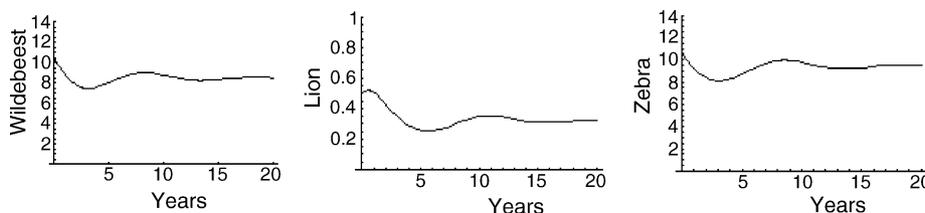
**Fig. 2 – Path of a trajectory with logistic growth and mutualism. The equilibrium at (7.336,0.343,8.076) is an attracting spiral point. The populations stabilize at this point only after approximately 80 years.**

to the number of killings taking place. The Lotka–Volterra predator–prey model, and therefore all the models above suggest that the number of prey killed is linearly dependant on the number of prey available. Normally, however, the feeding relation is a function of both predator and prey biomass, which can include the effects of relative “fullness” of a predator. In 1959, [Holling \(1965\)](#) was the first eco-biologist to classify functional response into three types, of which the Type II is applicable here. In his models, he allows for the time needed by a predator to kill and consume each prey, as well as the lapse in time before it is hungry again. This is expressed as a limiting factor  $1/(1 + mx)$  in the predation term of  $y$ , with the value of  $m$  determined by the population size of the predator. This phenomena is also recognized by [May \(1973\)](#) and [Pimm \(1991\)](#).

It is a well-known fact that a lion does not kill if it is not hungry. It will primarily kill to feed, therefore, the predation term in the equation describing lion dynamics will depend on both the prey and predator densities, as well as Type II functional response. When this principle is introduced to the previous three species model, we have

$$\begin{aligned} \frac{dx}{dt} &= 0.405x - 0.81xy + 0.015xz, \\ \frac{dy}{dt} &= -1.5y + 0.125(xy + yz)/(1 + 0.5y), \\ \frac{dz}{dt} &= 0.34z - 0.75yz + 0.02xz \end{aligned}$$

As expected, this limiting factor dampens the population growth of the lion, which in turn is advantageous to the prey species. [Fig. 3](#) shows very clearly that all three populations



**Fig. 3 – Population-time graphs of model with Type II functional response of lion show eventual stability, but do not fit census data.**

now experience smaller fluctuations, stabilizing at the attracting spiral point (7.34;0.35;8.07) after approximately 20 years.

This is a large improvement in fitting the model to the trends observed in the data, but does not explain the phenomenon of the zebra’s significant recovery to reach its carrying capacity in approximately 10 years’ time, while the wildebeest population lagged behind for several years before recovering.

### 3.5. Seasonal calving

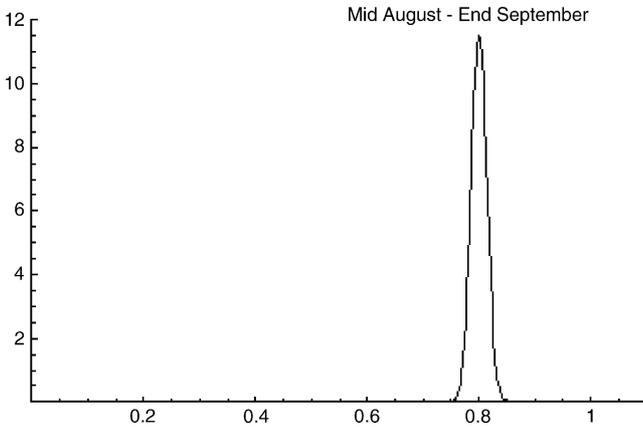
According to [Smuts \(1982\)](#) and [Starfield et al. \(1976\)](#) “... in the Kruger Park zebra have no preferred breeding season, while wildebeest have a very distinctive calving season during spring.” The effect of wildebeest delivering calves only during a “discrete” period per year while zebra presents a “continuous” reproduction of offspring may explain the difference in their rates of recovery. The periods of reproduction–non-reproduction of the wildebeest could simply be represented by a step function, but that would imply a definite on–off switch for births, which is not what we observe in nature. Another option is to use the properties of the sinusoidal function to present a smooth curve, as often applied to fluctuating rainfall patterns with good, average and bad years. Clearly this approach is also not suitable for a situation where a population of herbivores experience one peak in their calving season. The following argument is plausible for wildebeest in the subtropical climate of the Kruger Park: in early spring some cows will start dropping calves, the incidence will then pick up and peak within an approximate 2-week period of the calving season, after which there will still be a few late deliveries for another 2 weeks or so. The rest of the year shows practically no new births.

In order to model this pattern effectively, a Gaussian distribution over a 1-year period (that is  $t \in [0,1]$ ) is considered. Taking the mean  $\mu = 0.8$  to represent the peak of the wildebeest calving season in late August to early September, we have a calving season of approximately 6.2 weeks stretching from mid August to end September. The calving season is described by the Gaussian function

$$f(t) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(1/2)(t-0.8/\sigma)^2}$$

$((t-0.8)/\sigma)^2$  likewise below

The area included by the curve of the Gaussian function and the positive x-axis is approximately  $0.99973 \approx 1$  square unit if  $\sigma = 0.014$ . In practical terms this area represents the growth parameter of the species during each year. In order to correct this for our model with a growth parameter of 0.405 for wildebeest now concentrated in an approximate 6-week



**Fig. 4 – Scaled Gaussian curve includes and area of 0.405 square units, representing seasonal wildebeest calving from mid August to end September each year.**

calving season, the function  $g(t)$  is the growth parameter for wildebeest to be introduced in the model, where

$$g(t) = 0.405 \left( \frac{1}{\sqrt{2\pi(0.014)^2}} e^{-(1/2)(t-0.8/0.014)^2} \right)$$

This is depicted in Fig. 4.

The resulting model for wildebeest, lion and zebra is

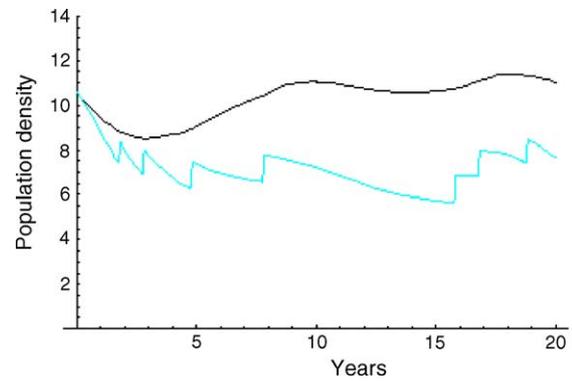
$$\frac{dx}{dt} = g(t) \left( 1 - \frac{x}{12} \right) - 0.81xy + 0.015xz,$$

$$\frac{dy}{dt} = -1.5y + 0.125(xy + yz)/(1 + 0.5y),$$

$$\frac{dz}{dt} = 0.34z \left( 1 - \frac{z}{12} \right) - 0.75yz + 0.02xz$$

The population growth patterns produced by this model, compared in Fig. 5, suggest that seasonal calving might have been responsible for the slow recovery of the wildebeest numbers. Note that the seasonal calving of wildebeest causes an erratic growth line over time, while the zebra population is represented by the smooth curve. It is also clear from these graphs that zebra numbers recovered to almost carrying capacity in a period of 10 years while the wildebeest lagged behind.

However, when the output of the model is compared to census numbers of the two species, the fit is not satisfactorily. This is illustrated in Fig. 6, where the scatter plot on the respective population-time graphs of the wildebeest and zebra indicates census numbers. Note that after 15 years the data and model



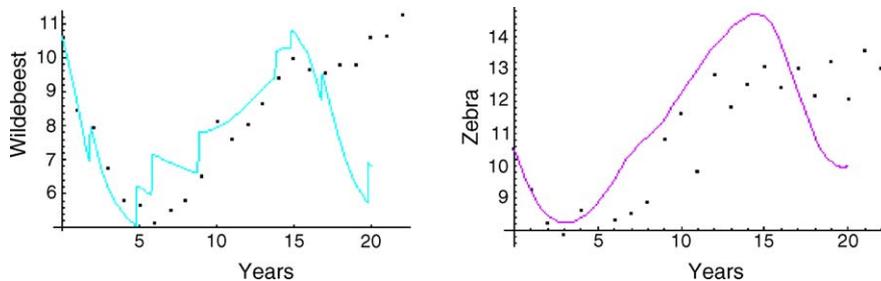
**Fig. 5 – Comparison of wildebeest (erratic curve) and zebra (smooth curve) densities of model that includes the effect of seasonal calving.**

predictions diverge significantly. It suggests that the model traces the path of a noisy sinusoidal curve, whereas, the data does not display these dynamics.

It is apparent that the model does not comply with its objectives to mimic and describe population dynamics of wildebeest and zebra accurately. The questions arise: did we misinterpret some information, or have we left out important information known about the system?

### 3.6. Cropping of lion

An important fact has not yet been taken into account. A cropping programme for lion was introduced in the Kruger Park between the years 1976 and 1986, as reported in depth by Smuts (1982). According to this report, the aim of the cropping was to reduce lion numbers to such an extent that it would allow the wildebeest and zebra populations to recover. The quota for culling was based on intuition of the field workers and not on the linear or quadratic approach to cropping, as suggested by Starfield and Bleloch (1986) and Fay and Greeff (1999b,c). According to Smuts (1982), the lion population in the total area of Kruger Park fluctuated between 1500 and 2000, and approximately 110 lion were culled per year over this period. Hence the cropping term to be introduced to the equation describing the population dynamics of lion is not taken as a function of the present population density, but as the constant ratio 110:2000. Since practically no cropping of lion was done before 1976, but was initiated in 1976 and then discontinued in 1984, it would be reasonable to use a step function  $v(t)$  to represent removal of a constant number of lions per year



**Fig. 6 – Wildebeest and zebra census numbers (scatter plots) compared to model output with seasonal calving (solid lines).**

over this period, where

$$v(t) = \begin{cases} 0, & 0 \leq t < 4 \\ 0.055, & 4 \leq t < 12 \\ 0, & t \geq 12 \end{cases}$$

Smuts also reports on nomadic prides entering the region when lion numbers decrease and prey is available. He estimates the influx at approximately 20 nomadic lions whenever the lion population drops to less than 300. The function  $v(t)$  is expanded to include this phenomenon with the additional statement where  $\varepsilon \approx 20/2000$  represents the movement of nomadic lions:

$$\text{If } y(t) < 0.3, \quad v(t) \leftarrow v(t) - \varepsilon$$

With the inclusion of  $v(t)$  in the equation describing the lion dynamics, the model to be evaluated is

$$\frac{dx}{dt} = g(t) \left( 1 - \frac{x}{12} \right) - 0.81xy + 0.015xz,$$

$$\frac{dy}{dt} = -1.5y + 0.125(xy + yz)/(1 + 0.5y) - v(t),$$

$$\frac{dz}{dt} = 0.34z \left( 1 - \frac{z}{12} \right) - 0.75yz + 0.02xz$$

Model output now mimics the census numbers closely for 15 years, as illustrated in Fig. 7, which is more than satisfactorily, considering the assumption that all exterior factors will remain constant.

According to Murray (1993, p. 375) it would not be realistic to expect even basic parameters such as growth rates of populations to be stable over such a long period.

The model output for lion population densities in the central area of the park also coincides with the expected decrease due to cropping, and recovery after termination of cropping. It is worthwhile mentioning that a closer investigation into the choice of the constant cropping parameter adopted by management,  $v(t) = 0.055$ , yields interesting results that correspond mathematically to what is reported in literature on possible instability of systems due to constant cropping: Testing the above system with slightly changed cropping parameter values for constant cropping of lion, a bifurcation is observed when  $v(t) > 0.06142$ , predicting uncontrolled growth of the prey population and extinction of lion after 15 years. In practical terms this implies that if 122 lion have been cropped for a period of 15 years, the results could have been disastrous. The

interested reader is referred to Fay and Greeff (1999a,b) and Starfield and Bleloch (1986) for a discussion of the dangers of constant cropping often implemented by field rangers.

### 3.7. Conclusion

It would be unreasonable to expect any model to fit the census data given in Table 1, perfectly or over a long period, when parameter values are expected to change. It is also generally accepted that census estimates are never 100% correct and may show a deviation of up to 20%. Thus our estimates of parameters are only well-informed guesses at best. Starfield and Bleloch (1986) sum it up with: “We can never really validate the sort of model that we have built, we can only hope to gain confidence in it.” In building this model we were successful in the sense that the model convincingly mimics the trend over a period of more than 15 years, which enables us to think usefully about the problem. It also promotes conceptual analyses of phenomena not clearly accounted for by the model, yet explained when analyzing model behaviour, for example:

- The erratic behaviour in the population curve for wildebeest indicates that peaks are evident at regular intervals, after each calving season.
- The amplitudes of these jumps are not constant, since they are dependent on the population size just prior to the calving season.
- The lion population at times seems to be too low, but has probably been reinforced by nomadic prides when prey numbers increase, as reported by Smuts (1982).
- An undercount of zebra numbers is suspected for the period 1976–1983: after abundant rainfalls, zebra will utilize areas with taller grass that makes counting more difficult, while wildebeest keep to shorter grass (Smuts, 1982; Starfield and Bleloch, 1986). This may explain model misfits to census data over this period.
- Model deviation from actual census numbers after 15 years may be due to changing dynamics or unstable exterior factors present in the ecological situation.

In this modelling exercise the deterministic approach to model three species interaction have been employed, in preference to a stochastic approach. The specific nature of the study and the number of parameters necessary to model the population dynamics contributed to this decision. The questions that immediately arise are:

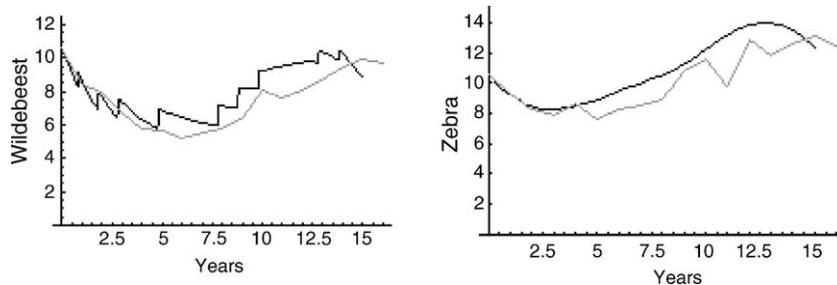


Fig. 7 – The model output (grey levels) fitted to census numbers (solid lines) for wildebeest and zebra. The lion population–time graph is not shown, but is more or less stable with small fluctuations between 300 and 500.

- How “good” are the parameter estimates included in the model?
- What measure of confidence can be assumed for model predictions?
- How sensitive is the model to small increments in parameter values?

To ensure that the specific model is robust and not overly parameter-dependent, an inductive study of error analysis has been undertaken and the degree of confidence that can be placed on the model has been investigated. The results are reported in [Fay and Greeff \(2006\)](#).

We trust that this practical exercise will be useful to young modellers, either in terms of mathematical (mis)interpretation of ecological information or stimulating innovative thinking about an old field of research.

## Acknowledgements

This research was supported by the National Research Foundation, South Africa (Grant number 2054454) since 1999. The authors thank the Technikon Pretoria (now partner in the merged Tshwane University of Technology), the University of Southern Mississippi, and personnel of the Kruger National Park for their support and useful suggestions. We also thank the reviewers and editor of *Ecological Modelling* for their comments regarding the improvement of this paper.

## REFERENCES

- Arditi, R., Ginzburg, L.R., 1986. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 262–311.
- Azar, C., Holmberg, J., Lindgren, K., 1995. Stability analysis of harvesting in a predator–prey model. *J. Theor. Biol.* 74 (1), 13–19.
- Boyce, W.E., Diprima, R.C., 1992. *Elementary Differential Equations*. Wiley, New York.
- Bothma-Du Preez, B.L.J., 1996. *Game Range Management*. J.L.v. Schaik, Pretoria.
- Costa, M.I.S., Kaszkurewicz, E., Bhaya, A., Hsu, L., 2000. Achieving global convergence to an equilibrium population in predator–prey systems by the use of discontinuous harvesting policy. *Ecol. Modell.* 128, 89–99.
- Dai, G.R., Tang, M.X., 1998. Coexistence region and global dynamics of a harvested predator–prey system. *SIAM J. Appl. Mathemat.* 58 (1), 193–210.
- Fay, T.H., Greeff, J.C., 1999a. Lion and wildebeest: a predator–prey model. *Mathemat. Comput. Edu.* 25 (2), 33–45.
- Fay, T.H., Greeff, J.C., 1999b. Nyala and Bushbuck: a competing species model I. *Mathemat. Comput. Edu.* 33 (2), 17–26.
- Fay, T.H., Greeff, J.C., 1999c. Nyala and Bushbuck: A competing species model II. *Mathemat. Comput. Edu.* 33 (2), 26–35.
- Fay, T.H., Greeff, J.C., 2006. Testing the model for one predator and two mutualistic prey. *Ecol. Modell.*, in press.
- Gui, Z., Ge, W., 2005. The effect of harvesting on a predator–prey system with stage structure. *Ecol. Modell.* 186 (3), 340–345.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Confronting Models with Data*. Princetown University Press.
- Holling, C.S., 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Ent. Soc. Can.* 45, 1–60.
- Jørgenson, S.E., 1988. *Fundamentals of Ecological Modelling*. Elsevier, Amsterdam.
- Křivan, V., 1998. Effects of optimal antipredator behaviour of prey on predator–prey dynamics: role of refuges. *Theor. Popul. Biol.* 49, 265–290.
- May, R.M., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- Murray, J.D., 1993. *Mathematical Biology*. Springer–Verlag, New York.
- Overton, W.S., 1984. A strategy of model construction. In: Hall, C.A.S. (Ed.), *Ecosystem Modelling in Theory and in Practice*, 5. Wiley, New York, pp. 52–53.
- Pimm, S.L., 1991. *The Balance of Nature?* University of Chicago Press, Chicago.
- Smuts, G.L., 1982. *Lion*. Macmillan South Africa Publishers Ltd. (Pty).
- Song, X., Chen, L., 2002. A predator–prey system with stage structure and harvesting for prey. *Acta Math. Appl. Sin.* 18 (3), 423–430.
- Starfield, A.M., Smuts, G.L., Shirly, J.D., 1976. A simple wildebeest population model and its application. *South African J. Wildlife Resour.* 6 (2), 95–98.
- Starfield, A.M., Bleloch, A.L., 1986. *Building Models for Conservation and Wildlife Management*. Macmillan Publishing Company, Brisbane.
- Tschirhart, J., 2004. A new adaptive system approach to predator–prey modelling. *Ecol. Modell.* 176 (3/4), 255–276.
- Wisdom, M.J., Mills, L.S., Doak, D.F., 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81 (3), 628–641.